



# Asymmetric Response to Heterotypic Distress Calls in the Lizard *Liolaemus chiliensis*

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## Abstract

The weeping lizard, *Liolaemus chiliensis*, emits distress calls when trapped by a predator. Conspecific lizards respond to such calls with prolonged immobility, which may increase their probability of remaining undetected by a predator. This benefit, however, depends on the ability to react to the alert message of the call, which may be impaired by natural variation in the calls. The distress calls of *L. chiliensis* show geographic variation, and here we tested the response of two geographically distant populations (>700 km apart) to local (homotypic) and non-local (heterotypic) distress calls; if populations are finely tuned to their local calls, they may not be able to respond to heterotypic calls. We found that geographic variation in calls affects the lizards' response, but this effect was population dependent; whereas southern lizards responded to calls of both populations, the northern lizards only reacted to homotypic distress calls. The factors that determine this asymmetric response to heterotypic calls are unclear and we discuss three hypotheses that have a common component in the difference in body size between the tested populations, which seems to play a key role in determining the response to distress calls in this species.

## Introduction

Many prey species emit distress calls when they are physically constrained by a predator (Caro 2005; Magrath et al. 2015). This type of vocalization has evolved independently several times in tetrapods, including in amphibians (Hödl & Gollmann 1986; Franzen & Glaw 1999; Toledo & Haddad 2009), crocodylians (Vergne et al. 2009; Bönke et al. 2015), lizards (Frankenberg & Werner 1992; Labra et al. 2013 and cited literature therein), and birds and mammals (Caro 2005). Most studies on these calls have been concentrated on birds and mammals, which had strengthened our understanding on the function and evolution of these calls (Neudorf & Sealy 2002; Caro 2005; Martin et al. 2011; Lingle et al. 2012). However, the widespread occurrence of distress calls across taxa may reflect their adaptive value for prey species, as calls may increase not only the survival probabilities of the prey itself but also of its conspecifics, due to the behavioral changes that calls

induce in predators and prey conspecifics (Högstedt 1983; Caro 2005).

Predators can be startled by distress calls and may release the captured prey (Neudorf & Sealy 2002). Calls may also attract secondary predators that attempt to steal the taken prey (Smith 1977), or force the primary predator to escape to reduce its own predation risk (Morse & Balsler 1961; Högstedt 1983; Schuett & Gillingham 1990). All this may create escape opportunities for the prey. Conspecifics can likewise respond to calls by approaching and mobbing the predator, which then may release the caught prey (Russ et al. 1998). Nevertheless, conspecifics can also reduce their own predation risk by reacting to calls and displaying antipredator behaviors, such as immobility (Vergne et al. 2011; Hoare & Labra 2013) or escape (Conover & Perito 1981). The opportunity for prey individuals to reduce their own predation risk by responding to the alert message of distress calls would be a strong selective pressure for the evolution of eavesdropping on heterospecific calls (Carter et al.

2015; Magrath et al. 2015). Remarkably, eavesdropping is facilitated by the conservative or convergent characteristics of distress calls across taxa (e.g., a rich harmonic structure; Jurisevic & Sanderson 1998; Lingle et al. 2012), but also because prey species seem to share similar strategies to decode the alert messages (Aubin 1991; Lingle et al. 2012).

Despite similarities in distress calls across taxa (Lingle et al. 2012), these vocalizations show intraspecific variation; individuals can produce more than one type of distress calls (Frankenberg & Werner 1984; Labra et al. 2013; Sicuro et al. 2013; Carter et al. 2015), and these can vary ontogenetically (Martins & Haddad 1988), individually (Franzen & Glaw 1999; Lingle et al. 2007), or geographically (Sicuro et al. 2013). Potentially, this intraspecific variation could make it hard for conspecifics to decode the alert message and fail to respond to the distress calls. Presently, very little is known about the consequences of intraspecific variation in distress calls, which contrasts with a considerable understanding of the implications of for example, geographic variation in acoustic signals involved in sexual selection (e.g., Gerhardt 2013; Wilkins et al. 2013). Nevertheless, considering that many species can react to heterospecific distress calls despite the interspecific variation (e.g., Lingle & Riede 2014), it is unlikely that intraspecific variation would constrain individuals to respond to the calls of their own species. Support for this proposition come from *Caiman yacare* (Sicuro et al. 2013) and the bat *Pipistrellus pipistrellus* (Russ et al. 1998), where it has been shown that individuals are able to respond to calls from other populations or colonies separated by a few km despite geographic variation in the calls. In these cases, the distances were rather short relative to the dispersal capabilities of the species and individuals may be regularly exposed to 'non-local calls'.

To test if the lack of contact between populations affects the ability of individuals to respond to non-local distress calls, we studied the responses of two geographically distant populations (>700 km apart) of the lizard *L. chiliensis*, to local (homotypic) and non-local (heterotypic) distress calls. We tested two populations, as evidence from the literature indicate that isolated populations may or may not evolve similar abilities to respond to heterotypic stimuli, and therefore, better information on the effect of geographic variation in distress calls is ensured by studying more than one population. There are three possible outcomes. One is that geographic variation may not disrupt the response and populations will react similarly

to calls independently of their origin. Alternatively, populations may be finely tuned to their local calls, precluding response to heterotypic calls. Finally, populations may experience different selective pressures, that cause an asymmetric ability to respond to heterotypic stimuli (Colbeck et al. 2010).

*Liolaemus chiliensis* is a native species to Chile (Mella 2005) that only vocalizes under predation risk; lizards rarely vocalize when they are exposed to a threat, such as a predator (pers. obs.), but they normally do so when constrained by a predator (Labra et al. 2013), giving rise to its common name: 'The weeping lizard' (Donoso-Barros 1966). This lizard generally respond to acoustic stimuli by becoming immobile, but the duration of the motionless period is much longer when lizards are exposed to distress calls than to a control acoustic stimulus (Hoare & Labra 2013). This prolonged immobility may reduce the lizards' possibilities of being detected, not only by visually oriented predators, as it has been shown for diverse taxa (e.g., Brodie 1977; O'Keefe et al. 1998), but also by more chemically oriented predators, such as snakes (e.g., Leal & Rodríguez-Robles 1995; Nishiumi & Mori 2015). Among the potential predators of *L. chiliensis* (snakes, raptors, and carnivores), the two most likely are the raptor *Falco sparverius* and the snake *Philodryas chamissonis*, as they include the highest percentage of lizards in their diets (Yáñez et al. 1980; Jaksic et al. 1981, 1982; Ebensperger et al. 1991; Greene & Jaksic 1992). Both these predators hunt by using a sit and wait strategy, and movement is a key factor for them to detect and attack prey (Collopy & Koplin 1983; Sarno & Gubanich 1995; Labra & Hoare 2015). Thus, immobility may be an effective way to reduce predation risk in *L. chiliensis*. Under natural conditions, *L. chiliensis* is highly cryptic when perching on scrub branches, remaining motionless, but alert, when it perceives perturbations (e.g., noise, approaching predator). When a predator gets too close, lizards escape inward into the bushes, but usually remain well positioned to observe through the branches; if the predator leaves, they restore their former positions (pers. obs.). Moreover, observations under laboratory conditions indicate that lizards decrease their movements after 'failed' attacks by dummies of *F. sparverius* and *P. chamissonis* (Constanzo 2012).

Considering that the distress calls of *L. chiliensis* have geographic variation in different characteristics such as in fundamental frequency and duration (unpub. data; see below), we tested if this variation constraints the response to distress calls to just within population.

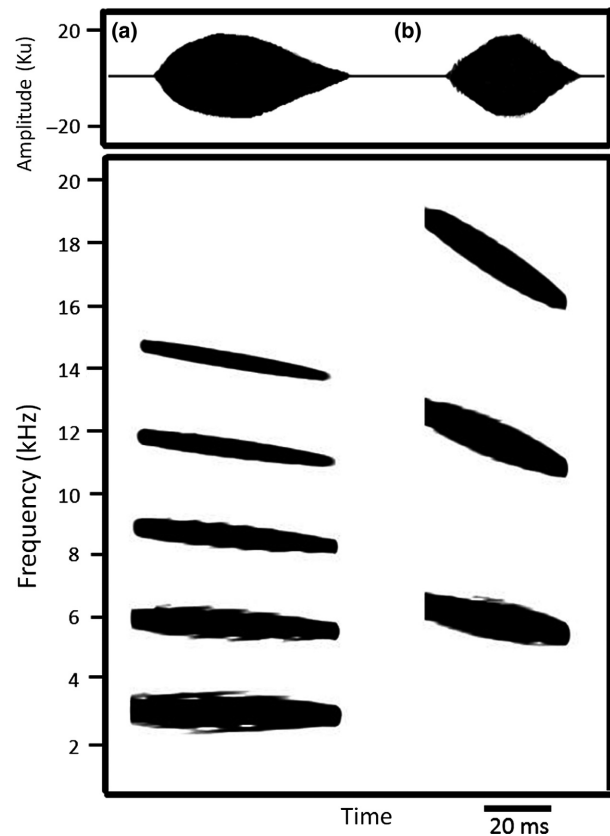
## Methods

We collected 36 adults of *L. chiliensis* during the spring and summer of 2012–2013 in sclerophyllous scrublands (Donoso-Barros 1966; Mella 2005). From a north-central area of the species distribution, Melipilla (33°42'23"S, 71°12'29"W; 170 m asl), we collected 21 individuals (10♀, 11♂; mean snout-vent length: 85.39 ± SE 1.83 mm). The other 15 individuals (8♀, 7♂; mean snout-vent length: 70.27 ± SE 1.69 mm) were from the southernmost area of the species distribution, Pucón (39°16'S, 71°58'W; 230 m asl). Snout-vent lengths differed between populations ( $t_{34} = 5.82$ ;  $p < 0.001$ ), but not between sexes in either of these populations ( $p > 0.05$ ).

In the laboratory, lizards were kept in an indoor vivarium with continuous ventilation and conditions resembling those recorded in the field during normal hot days, 13:11 L:D, with mean temperatures during this cycle of 33°C and 12°C. Lizards were housed individually in plastic enclosures (44.5 × 32 × 25 cm) that were equipped with climbing surfaces in the form of two windows covered by a plastic mesh in the front and in the lid. Enclosures had a sandy substrate, a wooden stick used as a perch, a pot for water, and an inverted pot for use as shelter and basking place. We provided water permanently, and food (mealworms dusted with vitamins) three times per week. Before the experiments, lizards remained undisturbed for at least 1 wk (except for feeding), and at the end of the experimental period, all individuals were returned in healthy condition to their georeferenced collecting points.

## Playback Experiments

Experiments were performed in a semi-anechoic room. Using a partially counterbalanced design, all lizards were submitted only once to each of the following four stimuli (treatments): (1) homotypic distress call, (2) heterotypic distress call, (3) homotypic white-noise stimulus, and (4) heterotypic white-noise stimulus. We controlled for intrapopulation variation in call characteristics (e.g., fundamental frequency) by making one synthetic distress call for each population (Fig. 1) based on average values of calls obtained in the previous season from individuals not included in this study (e.g., Velásquez et al. 2014). Call recordings were made at 35°C, the preferred body temperature of *L. chiliensis* (Labra et al. 2009), following a protocol previously used with this species (Hoare & Labra 2013; Labra et al. 2013). In brief, we evoked the distress calls by gently grasping a lizard with the



**Fig. 1:** Oscillogram (upper panel) and spectrogram (lower panel) of the synthetic distress calls of two populations of *Liolaemus chiliensis*: (a) north, Melipilla; (b) south, Pucón.

thumb and forefinger, and touching its snout with a finger for 2 min. Recordings were obtained using a directional microphone (Sennheiser ME 66; Sennheiser Electronic GmbH & Co., KG, Wedemark, Germany) and a portable stereo digital audio recorder (Tascam DR100; Tascam, Teac America INC, CA, USA) with a sampling rate of 44.1 kHz and 16-bit resolution, and files were saved in WAV format.

The characterization of the calls by population was based on simple calls (i.e., without nonlinear phenomena), as these were the most frequent (Labra et al. 2013; unpubl. data). The northern synthetic call averaged 247 calls from 30 individuals, whereas the southern one averaged 20 calls from eight individuals. Calls for both sexes were pooled, because there were no sexual differences in the parameters used to build the synthetic calls (e.g., fundamental frequency, duration, discernible harmonics in the frequency range of 0–21 kHz; Labra et al. 2013; unpubl. data). These parameters, however, differed significantly between populations (unpaired t-tests,  $p < 0.05$ ; unpubl. data). Call measurements were made with Raven Pro 1.4, and

acoustic stimuli were prepared using Adobe Audition 3.0. Because there is no information on the call characteristics that modulate the response of *L. chiliensis* to calls, we measured those characteristics described as relevant in triggering responses to distress calls in other species, for example frequency modulation, harmonic structure, frequency bandwidth amplitude (Aubin & Bremond 1992), fundamental frequency (Lingle et al. 2012; Teichroeb et al. 2013), and duration (Blumstein et al. 2008). We obtained the mean frequency value at the beginning and end of the first (fundamental) harmonic, and calls had down-modulated frequencies from 2.9–2.6 kHz and 6.3–5.3 kHz, for the northern and southern calls, respectively. In addition, we recorded the number of harmonics and their intensities to incorporate in the synthetic calls the average number of harmonics and the mean upper frequency limit recorded in each population up to 21 kHz (Fig. 1), with their corresponding mean intensities. In both populations, more than the 60% of the calls had the dominant frequency at the fundamental frequency (Labra et al. 2013; unpubl. data), therefore, we set the dominant frequency as the fundamental frequency. The maximum amplitudes of the call envelopes were at 25 and 21 ms for the northern and southern calls, respectively (Fig. 1). Finally, we created two white-noise stimuli (i.e., acoustic stimuli with a broad range of frequencies, each one with equal energy), one for each population, having the mean duration of the population calls, 60 and 43 ms for the northern and southern populations, respectively.

Following the set-up of Hoare & Labra (2013), stimuli were played back using a loudspeaker (Behringer, Zhongshan, China) placed on the floor, 15 cm in front of the window of the enclosure, the distance at which vocalizations were recorded and the shortest distance at which we have seen lizards in the field (per. obs.). The intensities of the stimuli were set at 51 dB sound pressure level measured at the center of the experimental enclosure, based on the call intensities previously recorded with a sound level meter (Brüel & Kjaer 2230 Sound & Vibration Measurement, Nærum, Denmark). The loudspeaker was connected through an amplifier (NAD Electronics 3020i; NAD Electronics International, Pickering, Canada), to a portable media player (iPod Nano A1320; Apple, Cupertino, CA, USA) to playback the stimuli.

At the vivarium, 10 min before starting the experiments, we removed from the maintenance enclosure of the tested individual the water container and the stick, but kept the refuge, and replaced the plastic lid by a sheet of glass (37 × 30 cm) to film the lizard.

Thereafter, we transported this enclosure with the lizard to the experimental room. During the experiments, enclosures were maintained at 35°C and at the end of the trial, we measured the cloacal temperature of the tested lizard. If temperature was not close to the species selected body temperature ( $35 \pm 2^\circ\text{C}$ ), the trial was discarded and repeated another day to avoid differences in behavior due to variation in body temperature. At the end of each trial, we restored the maintenance enclosure, and the tested lizard was kept undisturbed at the vivarium for at least 3 d before the next experiment (except for feeding).

We filmed the lizard's behavior using a video camera placed above the experimental enclosure. Recording began just after the lizard made the first tongue flick, which mark the onset of chemical exploration, and the experiments lasted 12 min plus the duration of the acoustic stimulus. Experiments had three stages: (1) pre-stimulus, the first 6 min after start of the recording, (2) stimulus, the period when the acoustic stimulus was played back, lasting 1.892 and 1.829 s for the northern and southern stimuli, respectively, and (3) post-stimulus, the final 6 min after stimulus. The acoustic stimulus was composed of three identical sounds (call or white-noise stimulus) separated by two silent periods of 0.7 and 1 s, which were within the range of the recorded silence periods when animals emitted distress calls. From the video records and using JWatcher (Blumstein et al. 2000), we scored during the pre- and post-stimulus periods four variables (chemical exploration, movements, time escaping, and time in the front half of the enclosure; for definitions see Table 1), and measured the latency to activity in the post-stimulus period (Table 1). In most trials (98%), lizards did not display any behavior during the short duration of the stimulus (<2 s), and therefore this period was not analyzed.

We determined the behavioral changes induced by the acoustic stimuli by computing the post- to pre-stimulus difference (i.e., post-stimulus values minus pre-stimulus values) of the four behavioral variables recorded in these two stages. Data from both sexes were pooled, as preliminary tests indicated no sexual differences in any of the recorded variables. The effect of the population (north vs. south), type of acoustic stimulus (call vs. white-noise stimulus), the origin of the acoustic stimulus (homotypic vs. heterotypic), and their interactions upon the studied variables were analyzed using partially nested three-way repeated-measure ANOVAs, with type and origin of the acoustic stimuli as within-subject variables (repeated-measurements), and population as between-subject variable. Analyses were followed by *post hoc*



**Table 1:** Behaviors recorded for *Liolaemus chiliensis* from videotapes. The first behavior was measured as the number of times and the remainder as the total time that lizards exhibited the behavior

Behavior	Description	Reference
1. Chemical exploration	Number of samplings of chemicals present in the environment, which included the number of tongue flicks and the rarely observed (<1%), mouth gaping	(Hoare & Labra 2013)
2. Movements (s)	Index of exploration that included the total time that animals made movements (e.g., walking, changing the position, scanning), but excluded motions that arose from other behaviors recorded (time escaping and chemical exploration)	(Hoare & Labra 2013)
3. Time escaping (s)	Time spent running, rubbing the snout against the enclosure walls, attempting to climb the walls, and digging the substrate	(Font & Desfilis 2002)
4. Time in front of the enclosure (s)	We divided virtually the enclosure into two halves and recorded the time that lizards spent in the front half (next to the window), which was closer to the source of the acoustic stimuli	Present study
5. Latency to activity (s)	Period of complete immobility after the stimulus, which ended when the lizard displayed any behavior that broke the immobility (e.g., escape attempt, chemical exploration, change of position, walking)	(Hoare & Labra 2013)

Fisher LSD tests. The movement variable was log transformed to ensure normality of the residuals. The residuals of all variables appeared homoscedastic and normally distributed.

## Results

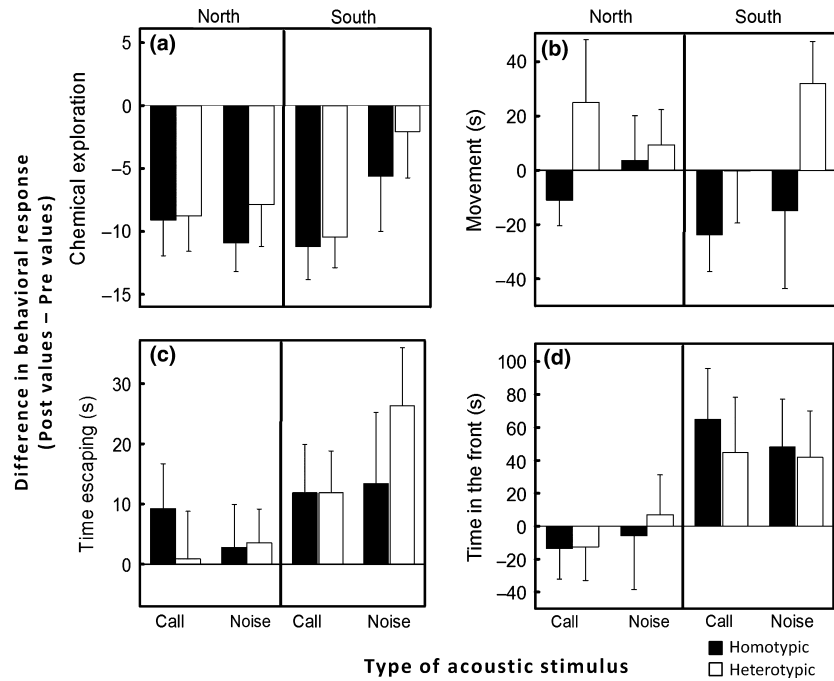
The chemical exploratory behavior was the only variable unaffected by any of the factors included in this study (Table 2), showing always a decrease after the stimuli (Fig. 2a). The three other variables recorded during pre- and post-stimulus were affected differentially by the studied factors (Table 2), and the estimates of their changes are in Fig. 2: movement (Fig. 2b), time escaping (Fig. 2c) and the use of the front part of the enclosure (Fig. 2d). The movement was only modulated by the origin of the stimuli (Table 2); independent of the population, lizards decreased their movements after homotypic stimuli, whereas heterotypic stimuli induced an increase in movements (Fig. 3a). The time escaping showed a

tendency ( $p = 0.051$ ) to be modulated by the interaction between the type of stimulus and population (Table 2); after being confronted with white-noise stimuli, the southern lizards tended to escape more than the northern lizards (Fig. 3b). Remarkably, lizards did not use the refuge during or after the acoustic stimuli. Finally, the use of the front part of the enclosure was only modulated by the lizard origin (Table 2); after the stimuli, southern lizards remained for longer closer to the stimuli source, the front of the enclosure, whereas the northern lizards did not modify the use of this section (Fig. 3c).

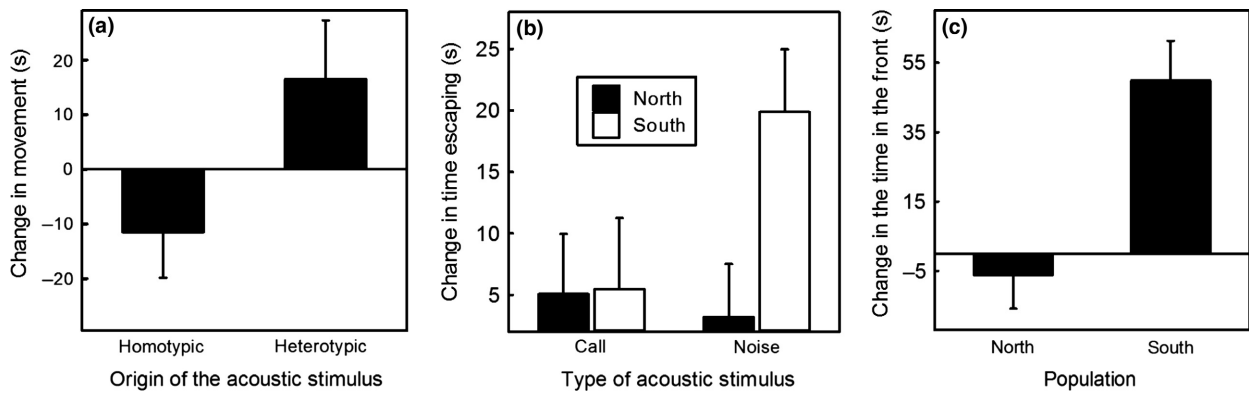
Lizards reacted to the different acoustic stimuli with immobility, but the duration of this immobility, the latency to activity after the stimulus, was significantly modulated by the different factors studied and their interactions (Table 2). The effect of the lizards' origin showed that the northern lizards remained immobile for longer than the southern individuals did. The type of stimulus also affected lizard behavior, with a longer period of immobility after calls than after the white-

**Table 2:** Results of the partially nested three-way repeated-measure ANOVAs to determine the effect of the population (pop.; north vs. south), type of stimulus (call vs. white-noise stimulus), origin of the stimulus (homo vs. heterotypic) and their interactions upon the behavioral changes (post-stimulus minus pre-stimulus values) of four variables (chemical exploration, movements -log transformed-, time escaping and time in the half front of the enclosure), and the latency to activity. Values shown are the F-statistics (p-value). The degrees of freedom of the tests were 1, 34. Statistically significant-tests are shown in bold. Sample size: 21 individuals from the north and 15 individuals from the south

	Chem. Expl.	Movements	Escaping	In the front	Lat. activity
Population	0.64 (0.427)	2.13 (0.153)	2.10 (0.157)	<b>14.24 (&lt;0.001)</b>	<b>4.70 (0.037)</b>
Type of stimulus	1.77 (0.192)	0.07 (0.795)	2.42 (0.129)	0.11 (0.917)	<b>18.92 (&lt;0.001)</b>
Origin of stimulus	1.22 (0.278)	<b>4.78 (0.042)</b>	0.52 (0.475)	0.02 (0.882)	1.77 (0.193)
Type of stimulus × Pop.	2.29 (0.139)	0.06 (0.805)	4.08 (0.051)	0.41 (0.527)	0.20 (0.655)
Origin of stimulus × Pop.	0.02 (0.899)	1.39 (0.246)	1.76 (0.193)	0.21 (0.651)	0.82 (0.372)
Type × Origin of stimulus	0.36 (0.553)	0.93 (0.341)	0.13 (0.720)	0.09 (0.768)	<b>4.69 (0.037)</b>
Pop. × Type × Origin of stimulus	0.00 (0.993)	1.96 (0.171)	0.12 (0.728)	0.00 (0.984)	<b>4.59 (0.039)</b>



**Fig. 2:** Behavioral changes (mean  $\pm$  SE) of four variables recorded in two populations (north and south) of *Liolaemus chiliensis*, when confronted with four acoustic stimuli. The horizontal line (zero) indicates the point where there is no change between the pre- and post-stimulus periods. Negative values indicate that after the stimulus, the behavior decreased in relation to the pre-stimulus condition. (a) Chemical exploration. (b) Untransformed data of movement. (c) Time escaping. (d) Time spent in the front part of the enclosure.

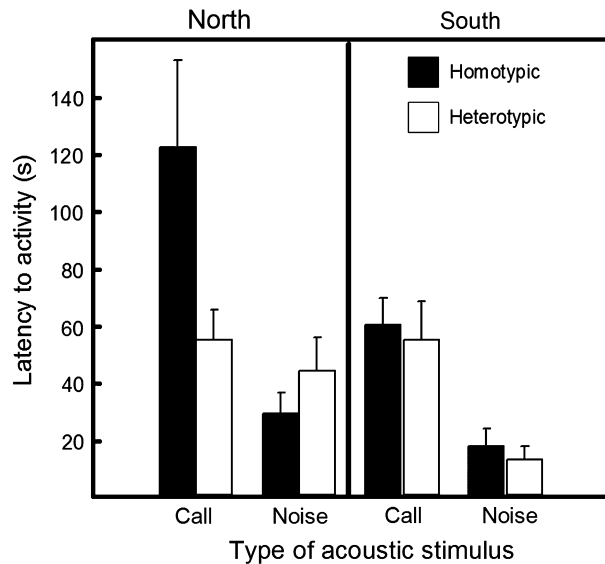


**Fig. 3:** Behavioral changes (mean  $\pm$  SE) of the three variables modulated by different factors analyzed in *Liolaemus chiliensis*. (a) Untransformed data of movement. Variable modulated by the origin of the acoustic stimulus (homo- vs. heterotypic). (b) Time escaping had a tendency to be affected by the interaction between the type of the acoustic stimulus (call vs. white-noise) and the population (north vs. south). (c) Time spent in the front part of the enclosure was affected by the lizard origin (north vs. south). The horizontal line (zero) indicates the point where there is no change between the pre- and post-stimulus periods.

noise stimuli (Fig. 4). The origin of the stimulus did not affect immobility, but there was a significant interaction with the other two factors (Table 2 and Fig. 4), as both populations reacted differently to the calls, depending on their origin. The northern lizards only reacted to homotypic call, behaving similarly when confronted to the heterotypic distress call and the two white-noise stimuli. In contrast, the southern lizards responded similarly to homo- and heterotypic distress calls, and the mean duration of the immobility was longer after calls than after white-noise stimuli.

**Discussion**

Individuals of *L. chiliensis* respond to conspecific distress calls with prolonged immobility (Hoare & Labra 2013), a reaction that may reduce their predation risk (e.g., Brodie 1977; Leal & Rodríguez-Robles 1995; O’Keefe et al. 1998). In the present study, we found that this response is affected by geographic variation in the calls. We found that the northern lizards only exhibited immobility when confronted with homotypic calls, whereas southern lizards exhibited



**Fig. 4:** Mean latency to activity (+ SE), the onset of any behavior after the presentation of the acoustic stimulus (call vs. white-noise stimulus), from different origins (homo vs. heterotypic), recorded in two populations of *Liolaemus chiliensis* (north vs. south).

immobility in response to both homo- and heterotypic distress calls. Overall, these results indicate, on one hand, that lizards do not require a previous exposition to heterotypic distress calls to react to them, and second, that populations seem not to be equally tuned to their calls, resulting in an asymmetrical non-local response to distress calls (Colbeck et al. 2010).

From the five behavioral measurements recorded (Table 1), only the latency to activity after the stimulus reflected a clear response to distress calls, as was previously reported (Hoare & Labra 2013). Staying immobile would allow individuals to remain undetected by the predator that is subduing a conspecific in the proximity, which can be particularly relevant for *L. chiliensis*, which tends to be highly cryptic in scrub branches, and movements may break this cryptic allowing predators to detect the lizards (e.g., Houtman & Dill 1994). In fact, lizards never ran or attempted to use the refuge during the stimuli presentation. After this period of immobility, the type of acoustic stimuli did not modulate the lizard behavior, probably because lizards did not receive more information on the predatory event (e.g., branch movements, more distress calls), and therefore, they restored their normal activities relatively soon. This may explain why the northern lizards did not show changes in the use of the area close to the source of the acoustic stimuli after its presentation. We postulate, therefore, that immobility may be the safest initial reaction of *L. chiliensis* to avoid a perceived threat

when confronted with a very short and acute alert of risk.

The factors behind the asymmetrical response to heterotypic calls in *L. chiliensis* are unclear, and we propose three not mutually exclusive hypotheses with a common component in the difference in body size between these populations. The first hypothesis proposes that populations have different levels of stressful conditions, which determines different responses to the alerts of predation risk. Usually, stressed animals are more responsive to threat (e.g., Martins et al. 2011; Journey et al. 2013), and predation is an important life threat (e.g., Bell et al. 2010). Presently, there is no information on the predation pressures experienced by the studied populations, but considering that the geographic distribution of the predators overlaps with both populations (Jaksić et al. 1982; Jaramillo 2005; Mella 2005; Iriarte 2007), these populations should have the same predators. However, even if they have the same predators, the southern population may experience a higher predation risk than the northern one, as smaller individuals tend to have higher predation risk *per se*, because they are easier to manipulate and can have a larger spectrum of predators than bigger prey (Caro 2005; Stankowich et al. 2014). In fact, the smaller body size of the southern population may facilitate attacks by unusual lizard predators such as birds, Passeriformes (Pérez & Avila 2005; Marín 2013; Salvador & Bodrati 2013; Bianchini 2014), and Piciformes (Ojeda & Chazarreta 2006). A higher predation risk for the southern lizards would explain their higher responsiveness to threats; they not only responded to homo- and heterotypic distress calls, but they also attempted to escape more when they were confronted with an unknown short acoustic perturbation (white-noise stimuli). Remarkably, however, southern lizards restored their activity faster than northern lizards (i.e., shorter latency to activity), and remained closer to the source of the stimulus, the front of the enclosure. Potentially, approaching the stimulus may be part of a mobbing behavior (Russ et al. 1998; Lee et al. 2015), or a learning process (Conover 1994; Griffin 2009; Carter et al. 2015), although there is no independent evidence of such behavior in *Liolaemus*.

The second hypothesis proposes that even if lizards decode the alert message of the distress calls, they only respond if calls convey information about a serious risk. Distress call parameters encode information on prey body size (Jurisevic & Sanderson 1998; Toledo & Haddad 2009; Martin et al. 2011; Vergne et al. 2012; Bönke et al. 2015), and indirectly, on the

predator body size, as prey and predator sizes are positively correlated (e.g., Costa 2009; Jonsson 2014). In case of *L. chiliensis*, the short duration and the high fundamental frequency of the southern call would encode a relatively small individual (Labra et al. 2013), and hence a relative small predator, which may not represent a real risk for a large (northern) lizard that consequently does not respond to the call. In contrast, the southern lizards with a potential broader spectrum of predator sizes, may respond to distress calls from individuals with a wider range of body sizes. Support for this proposition come from studies on alarm calls (i.e., vocalizations emitted by prey in the presence of a predator before any physical contact; Caro 2005), which show that small individuals (juveniles) respond to calls emitted by large (adults) and small individuals, whereas large individuals only react to calls from large individuals (Hanson & Coss 2001; Nakano et al. 2013; but see Blumstein & Daniel 2004).

The final hypothesis is that there is a matching between call characteristics and hearing sensitivities, and populations are tuned to the acoustic characteristics of their own distress calls (Manley et al. 2014; Chen et al. 2016), and specifically to the fundamental frequency (Teichroeb et al. 2013; Lingle & Riede 2014). Teichroeb et al. (2013) found a positive relation between the mean and the range of fundamental frequencies of mammalian distress calls. In two sympatric deer species, they also found a relation between the mean and the absolute tolerated variation of fundamental frequencies, and the species that had calls with higher fundamental frequency tolerated a wider absolute variation of this frequency in the calls, which included the heterospecific calls. In contrast, the species that had calls with a lower fundamental frequency, tolerated a narrower absolute variation in this frequency in the calls, and thereby did not include the heterospecific calls with a high fundamental frequency. In agreement with the Teichroeb et al. (2013) results, we found that the southern population, which has distress calls with high fundamental frequency, reacted to calls with a wider range of fundamental frequencies (i.e., homo- and heterotypic calls), whereas the northern population, which has calls with low fundamental frequency, only reacted to homotypic calls. In case of deer, however, neither the interspecific variation in the distress call characteristics nor the response that they elicited was related to differences in body sizes (Lingle et al. 2007; Teichroeb et al. 2013). In this lizard species, however, body size differences between populations may be the factor determining the interpopulation difference in the call

fundamental frequency; large lizards have low fundamental frequency. In addition, large individuals broadcast sounds at lower frequencies (Ryan & Brenowitz 1985), and tend to have a higher hearing sensitivity (Werner et al. 2008) due to their comparatively bigger receptor structures (Werner & Igic 2002). Experimental manipulation of the fundamental frequencies will clarify how essential this parameter is in triggering antipredator responses in *L. chiliensis*. In addition, it will also be necessary to determine if stimulus duration modulates the post-stimulus response, as lizards reduced their movements after homotypic call and white-noise stimulus, which have duration in common. Potentially the strategies may be to remain motionless under 'normal' (homotypic) duration, but to explore under 'abnormal' (heterotypic) duration.

Independently of the factors behind the asymmetrical response to heterotypic distress calls, the capability of the southern lizards to respond to distress calls with a wider range of fundamental frequencies may allow them eavesdropping calls emitted during predation risk by different sympatric prey species with which share predators (e.g., Magrath et al. 2015). Presently, there are well-known cases of non-vocal lizards that eavesdrop on calls from sympatric bird species with which they share predators (e.g., Ito & Mori 2010). Therefore, it is possible that a vocal lizard, such as *L. chiliensis*, may eavesdrop on heterospecific calls.

As far as we know, this is the first study that investigates the consequence of the intraspecific variation in distress calls in a lizard, and our data show that geographic variation can affect the response to heterotypic calls. In case of *L. chiliensis*, however, the body size difference between the studied populations may play an important role in modulating how individuals respond to this variation.

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